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Foraging strategy of nocturnal orb-web spiders (Araneidae: *Neoscona*) with special reference to the possibility of beetle specialization by *N. punctigera*

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Abstract — To clarify the foraging strategy of nocturnal orb-web spiders, we examined the relationship between prey items and foraging traits in four *Neoscona* species that spin typical orb-webs. Taxonomic composition of prey differed markedly among species; beetles occupied about 50% of prey in *N. punctigera* and *N. scylla*. As beetles are generally heavier than other prey, these differences could be due to the differences in kinetic energy absorption ability of webs and/or web stickiness. Comparison of the sympatric two species (*Neosocna punctigera* and *N. mellotteei*) with similar body size supported the above inference; mesh density and silk stickiness were higher in *N. punctigera* that captured more beetles, while microhabitat and other foraging traits were similar. These results suggest specialization to beetles in some nocturnal orb-web spiders.

Key words — nocturnal, prey items, foraging traits, growth rate, interspecific comparison

Introduction

Spiders belonging to the superfamily Araneoidea forage in a variety of light environments (Craig et al. 1994). Some species in this group forage only at night (Carico 1986), but with the exception of a few species that have highly specialized webs (e.g. *Pasilobus* sp. Robinson & Robinson 1975, *Mastophora* sp. Yeargan 1994, *Crytarachne* sp. Cartan & Miyashita 2000), their foraging strategies, such as the relationship between web properties and prey type, are not well understood. Previous studies have shown that aerial insects are less diverse at night than in the daytime (Nyffeler & Benz 1989, Speakman et al. 2000, Basset et al. 2001), and that moth and beetle species are more abundant at night (Herberstein & Elgar 1994, Speakman et al. 2000, Spagarino et al. 2001). However, moths and beetles are difficult to catch because of the presence of scales (Eisner et al. 1964) and their forceful struggling in the web (Nentwig 1982), respectively. Therefore web must have high stickiness and high kinetic energy absorption ability to capture these insects.

Here we show prey items and foraging traits of nocturnal orb-web spiders that weave ordinary orb-webs, and explore the possibility of prey specialization in these spiders. Firstly we examine the relationship between prey items and web properties in the four species of the genus *Neoscona*. These species spin ordinary orb-webs and are widely distributed in Japan (Tanikawa 1998). We focus on two important properties for capturing prey, i.e., kinetic energy absorption ability of web and web stickiness. Secondly, in order to assess the possible factors that may determine interspecific differences in prey items, we evaluated quantitatively the following foraging processes in two sympatric species *Neoscona punctigera* and *N. mellotteei*, i.e., web placement, web and silk properties and response to prey. Comparisons of sympatric species may allow us to reveal the causal relationship between prey items and foraging strategies since they will experience similar prey availabilities. Based on these results, we discuss how prey specialization can be achieved by nocturnal orb-web spiders.

Methods

Spiders and field sites

The four *Neoscona* species have a univoltine life cycle and overwinter as juveniles. *Neoscona scylla* starts foraging from early May to early July, *N. scylloides* from middle June to early August, *N. mellotteei* from early July to September, and *N. punctigera* from early July to middle September. These species begin spinning their webs just after sunset and remove them in the early morning. After web removal, they rest on a retreat constructed on twigs or leaves. Body length of adult females is about 13 mm in *Neoscona scylla*, 9 mm in *N. scylloides*, 7 mm in *N. mellotteei*, 10 mm in *N. punctigera* (Tanikawa 1998, personal observation).

Field survey was conducted at the forest edge in deciduous forests and a chestnut plantation in Namekawa-cho, Saitama prefecture, Japan. The deciduous forests habitat included tree species such as *Quercus acutissima*, *Quercus serrata*, *Morus bombycis*, *Castanea crenata*, *Styrax japonica*, and some herbaceous species including *Solidago altissima* and *Pueraria lobata*.

Prey items and orb web design in four *Neoscona* species

Prey survey was conducted at night every two weeks from June to September, 2004. All species were examined in the deciduous forest habitats, but as a result of low species abundance, observations of *Neoscona punctigera* were also made in a chestnut plantation. Prey upon which spiders were feeding, left wrapped in silk were collected using forceps and preserved in 70% alcohol. Spider body length (cephalothorax-abdomen length) was measured on the web using calipers. Later, we identified prey preserved in alcohol to order or suborder, and measured its body length. Wet prey weight was calculated from the prey length using order specific allometric equations from Tanaka (1991) and Shimazaki & Miyashita (2005); Stumpy Diptera $W(\mathrm{mg}) = 0.0403X(\mathrm{mm})^{2.42}$, Slender Diptera $W = 0.0693X^{1.59}$, Ant $W = 0.0011X^{4.42}$, Wasp $W = 0.0149X^{2.75}$, Homoptera $W = 0.0162X^{3.39}$, Hemiptera $W = 0.206X^{2.13}$, Lepidoptera $W = 0.0382X^{2.3}$, Coleoptera $W = 0.0813X^{2.6}$, Araneae $W = 0.069X^{2.43}$, Orthoptera $W = 0.2361X^{1.51}$. For prey orders for which no specific equations was available, prey weight was calculated using the general equation from Rojers et al. (1976); $W = 0.0305X^{2.62}$.

The following web and silk traits were recorded every two weeks from June to September in 2003 and 2004.

1) Mesh height of spiral silk: To calculate mesh height, we used the equation of Herberstein & Tso (2000).

2) Breaking strength of spiral silk and elongation of spiral silk: Silk traits were measured using unstressed webs collected by photographic slide mount. To measure breaking strength and elongation of silk, slide mount was fixed on a stand and small weights (each 20 mg) were hooked to a single thread of the web. Loading continued until the silk broke. We defined breaking strength as the weight that broke the silk, and elongation as the length that the thread was stretched to by this loading. Silk kinetic energy absorption was calculated as [breaking strength] × [elongation] (see Cartan & Miyashita 2000).

3) Sticky droplet diameter and sticky droplet density: To measure the diameter and density of droplets, we observed silk secured in slide mount using a light microscope. We defined droplet diameter and droplet density as [vertical diameter + horizontal diameter]/2 and the number of droplet per 1 μm, respectively. Silk stickiness was estimated by substituting these values into the equation of Opell (2002).

Breaking strength was measured within 6 hours, and elongation, sticky droplet diameter and sticky droplet density were measured within 24 hours after web collection. We measured spider body length with a caliper.

We performed one-way ANOVA to compare the prey weight and web traits among species. When data were not normally distributed, we analyzed these data after log-transformation.

Prey type and foraging strategy in two sympatric species

We examined prey item, prey capture rate, and web placement from July to September in 2004 in a chestnut plantation where *Neoscona punctigera* and *N. mellotteei* coexisted. Surveys of prey type and web placement were performed every two weeks while a survey of prey capture rate was performed every week. Just after sunset (around 19:00), we marked web placement of spiders. Then, we visited each spider every 45 minutes intervals until 1: 00, collected insects caught by the spiders, and measured web height, percentage of vegetation coverage around the web within 10 cm from the web plane, and spider body length. We defined prey capture rate as the number of prey captured per hour.

We examined web and silk traits as well as behavioral traits in both the chestnut plantation and the forest edge of deciduous forests. Web and silk traits examined were the same as in the "four species comparison". The behavioral traits examined were, 1) response time, 2) wrapping time of prey, 3) weights of wrapping silk. We artificially provided a vibration stimulus to the radii 10 cm below the hub with an electric tooth brush, and recorded the spider response using a video camera (SONY DCR-TRV18). We defined response time as the time from the start of plucking the web with its legs to reaching the brush. Wrapping time and weight of wrapping silk were measured by experimentally placing a beetle *Tenebrio molitor* (body length about 13 mm) onto the spider web. As spiders which continued to bite prey for longer than 30 seconds did not wrap it any more (personal observation), we defined wrapping time as the time from the start of wrapping to carrying the prey to the hub or continuing to bite the prey at wrapping point over 30 seconds. After recording the wrapping time by stopwatch, we removed the prey from the spider web, carefully unraveled the silk and weighed it on a microbalance (CAHN, C-33: accuracy level at 0.001 mg).

We performed t-tests to compare the prey weight and web traits between species. All statistical analysis was performed by using SYSTAT 8.0.

Results

Prey type and orb web design in four *Neoscona* species

Taxonomic compositions of prey differed significantly among species (Fig. 1, $\chi^2 = 125.994$, df = 15, $p < 0.001$); *Neocona punctigera* and *N. scylla* captured more Coleoptera than the other two species. *Neoscona punctigera* and *N. scylla* captured heavier prey than the other two species (Fig. 2, one-way ANOVA, $F_{(3,\,543)} = 19.855$, $p < 0.0001$, post hoc test with Bonferini adjustment).

Table 1 shows allometric equations between body length of spiders and their web and silk traits. We estimated kinetic energy absorption ability of web and web stickiness from the body length of the spider from which prey was collected by using allometric equations. Web kinetic energy absorption ability was calculated as [kinetic energy absor-

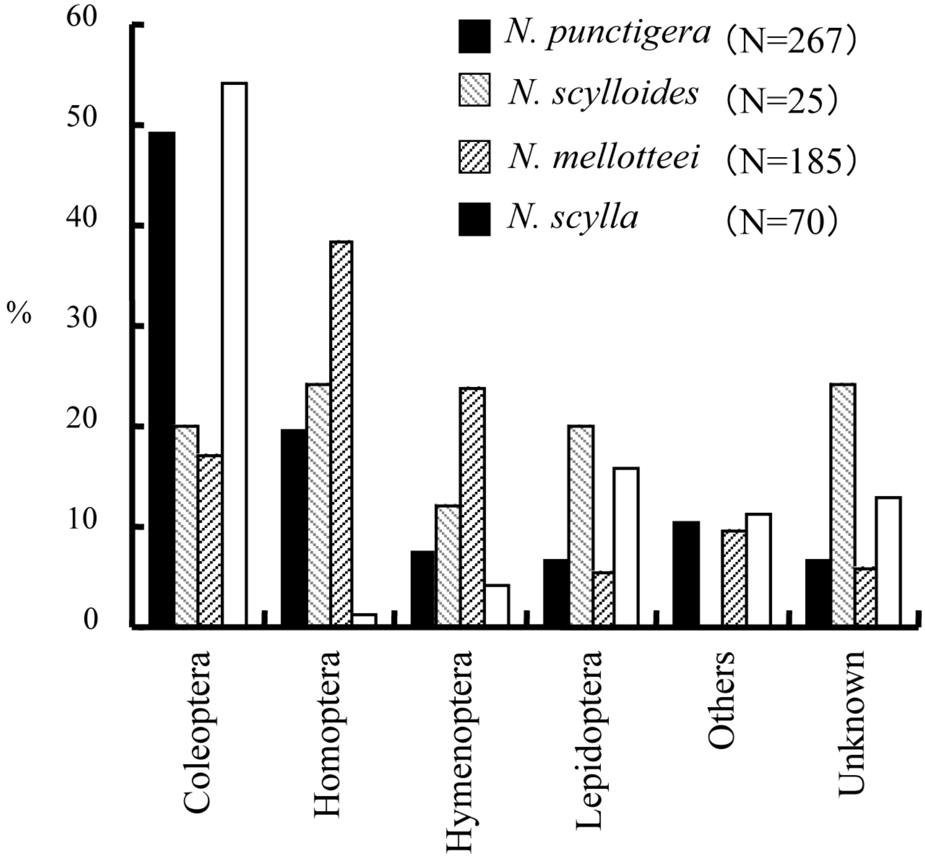

Fig. 1. Prey composition of four *Neoscona* species

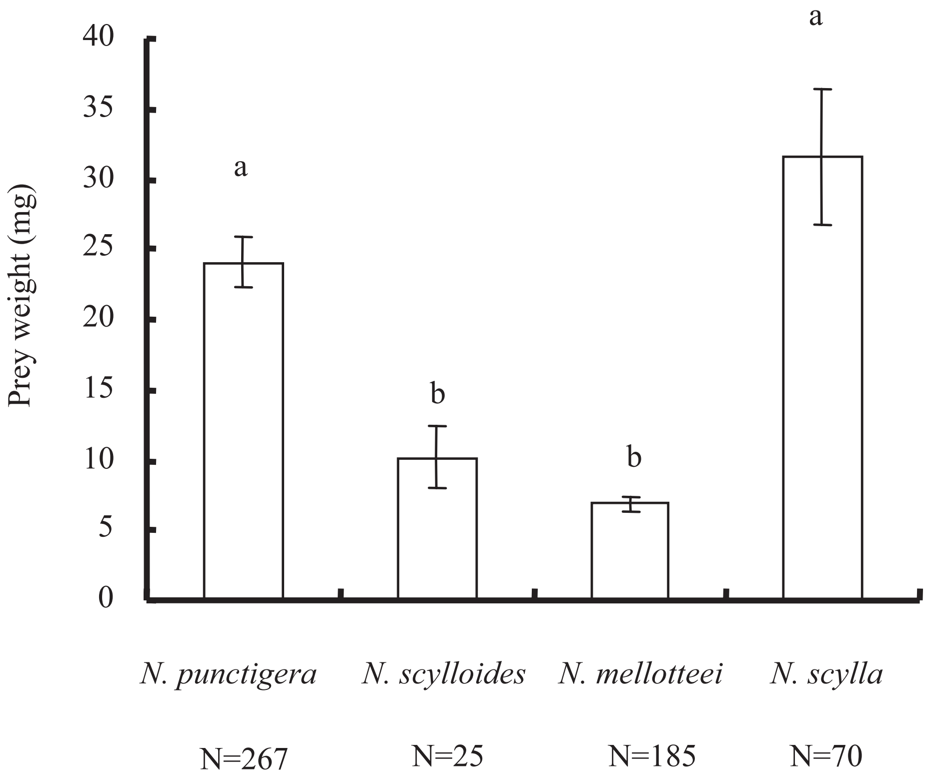

Fig. 2. Comparison of prey weight among four *Neoscona* species. Different symbols mean significant difference at the 0.05 level. Each error bar shows standard error.

ption ability of silk]/[mesh height]; web stickiness as [silk stickiness]/[mesh height]. Since there was no significant relationship between body length and kinetic energy absorption ability of silk for *Neocona mellotteei* (Table 2), we used the average value 69.7 (mg/cm).

Neoscona punctigera showed the highest web stickiness (Table 2 one-way ANOVA, $F_{(3,551)}=443.865$, $p<0.0001$, post hoc comparison with Bonferoni adjustment). *Neoscona punctigera* and *N. scylla* had higher energy absorption ability of webs than the other two species (Table 2 one-way ANOVA, $F_{(3,551)}=78.580$, $p<0.0001$, post hoc comparison with Bonferoni adjustment). *Neosocna punctigera* and *N. scylloides* were larger than *N. mellotteei* but smaller than *N. scylla* (Table 2 one-way ANOVA, $F_{(3,551)}=67.264$, $p<0.0001$, post hoc comparison with Bonferoni adjustment).

Prey type and foraging strategy in two sympatric species

To remove the possible effects of body size on prey items and microhabitat use of the two species, we used data of spider individuals whose body lengths range from 6.8 to 8.1 mm, for which there was no significant difference in spider length between the two species ($t=1.495$, df$=46$, $p=0.142$). Prey composition differed significantly between the species (Fig. 3, $\chi^2=6.835$, df$=1$, $p=0.012$, orders other

Table 1. Relationship between spider body length (X) and web and silk properties (Y) in four *Neoscona* species.

Species	Mesh height	Kinetic energy absorption of silk	Silk stickiness
punctigera	$\log Y=-1.126 \log X+1.785$, $F_{(1,50)}=101.295$, $p<0.0001$	$\log Y=2.739 \log X-0.419$, $F_{(1,33)}=22.609$, $p<0.0001$	$\log Y=0.792 \log X+0.533$, $F_{(1,27)}=34.044$, $p<0.0001$
scylloides	$\log Y=-0.861 \log X+1.488$, $F_{(1,28)}=46.373$, $p<0.0001$	$\log Y=1.591 \log X+0.427$, $F_{(1,17)}=7.521$, $p=0.014$	$\log Y=1.432 \log X-0.111$, $F_{(1,12)}=18.271$, $p=0.001$
mellotteei	$\log Y=-0.686 \log X+1.325$, $F_{(1,91)}=58.587$, $p<0.0001$	$F_{(1,41)}=0.791$, $p=0.379$	$\log Y=1.245 \log X+0.089$, $F_{(1,38)}=21.699$, $p<0.0001$
scylla	$\log Y=-0.763 \log X+1.434$, $F_{(1,90)}=150.819$, $p<0.0001$	$\log Y=1.58 \log X+0.515$, $F_{(1,32)}=7.793$, $p=0.009$	$\log Y=1.18 \log X+0.037$, $F_{(1,34)}=12.541$, $p=0.001$

Table 2. Body length and web traits in four *Neoscona* species. Different symbols mean significant difference (post hoc test with Bonferoni, $p<0.05$), and all values are represented by "mean±SE".

	punctigera (n=273)	*scylloides* (n=24)	*mellotteei* (n=188)	*scylla* (n=70)
Spider length (mm)	8.3 ± 0.1^b	8.0 ± 0.4^b	6.5 ± 0.1^c	10.5 ± 0.3^a
Web stickiness (μN/cm)	41.9 ± 0.3^a	30.3 ± 0.9^b	29.2 ± 0.2^b	30.0 ± 0.3^b
Web kinetic energy absorption ability (mg/cm)	275.0 ± 6.8^a	145.6 ± 5.4^b	165.0 ± 1.7^b	231.8 ± 5.0^a

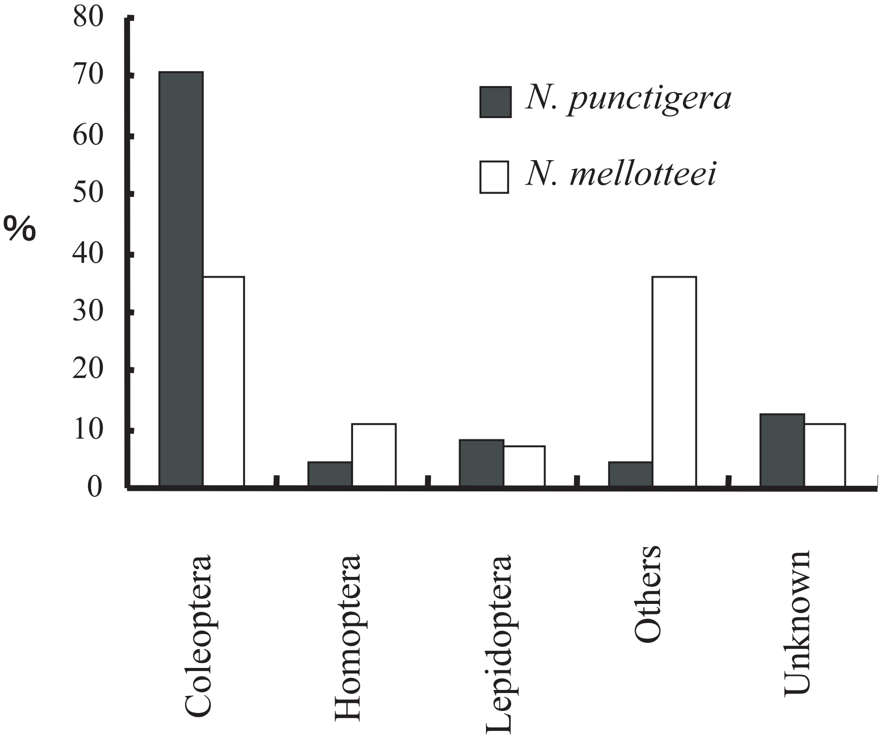

Fig. 3. Comparison of prey composition between two sympatric species.

than Coleoptera pooled), with *Neoscona punctigera* capturing more Coleoptera than *N. mellotteei*. Coleoptera consisted of Elatoridae, Curculionoidea, Carabidae. *Neocona punctigera* captured heavier prey than *N. mellotteei* (Table 3, but the prey capture rate did not differ between species (t-test, $t=0.246$, df=38, $p=0.807$). Both vegetation coverage and web height did not differ between species (Table 3).

We compared web and silk traits between species in the same body size range as above. *Neoscona punctigera* tended to show a larger mesh density and a higher silk stickiness compared to *N. mellotteei* (Table 3). *Neoscona punctigera* showed a higher web kinetic energy absorption ability and web stickiness than *N. mellotteei*, 1.65 times and 1.42 times greater, respectively.

We compared the response time to prey on the web between the species in the same body size range mentioned above, but weights of wrapping silk and wrapping time in the body length range of 7.4–10.4 mm. In this range, *Neoscona punctigera* was slightly larger than *N. mellotteei* (average±SE, *N. punctigera* 9.5±0.04, n=6, *N. mellotteei,*

Table 3. Comparison of prey weight and foraging traits between two sympatric species of *Neoscona*. All values are represented by "mean±SE".

		N. punctigera	*N. mellotteei*	*p*
Prey	prey weight (mg)	26.9±7.2 (n=22)	4.0±1.2 (n=26)	**0.002**
Microhabitat	vegetation cover (%)	60.0±8.2 (N=15)	67.6±6.6 (N=19)	0.468
	web height (cm)	123.8±8.3 (N=17)	134.9±8.3 (N=26)	0.371
Web trait	mesh height (cm)	0.40±0.04 (N=14)	0.50±0.031 (N=21)	**0.076**
Silk trait	silk strength (mg)	70.8±11.0 (N=13)	57.8±3.0 (N=36)	0.118
	kinetic energy absorption ability (mg/cm)	120.2±24.4 (N=11)	89.9±10.4 (N=36)	0.197
	stickiness (μN)	18.7±0.57 (N=9)	16.4±0.67 (N=29)	**0.074**
Behavioral trait	wrapping time (s)	209.7±31.4 (N=6)	204.1±29.7 (N=11)	0.907
	wrapping silk weight (mg)	0.74±0.14 (N=6)	0.59±0.09 (N=11)	0.351
	response time (s)	1.75±0.43 (N=28)	2.04±1.21 (N=7)	0.875

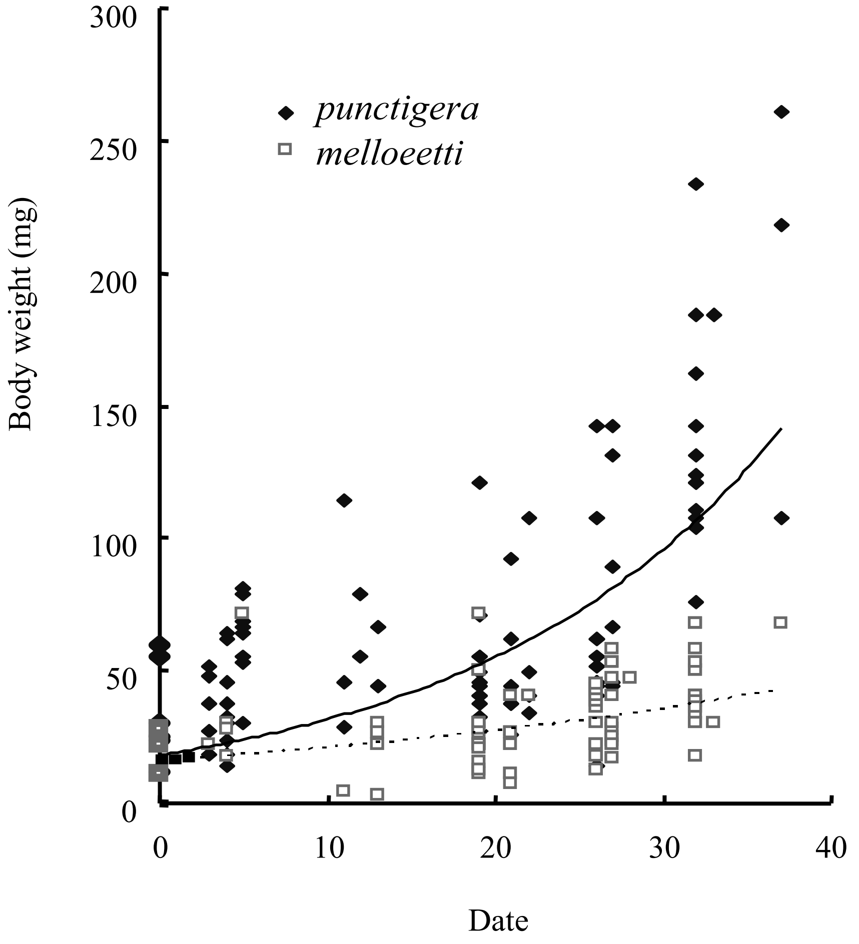

Fig. 4. Changes in spider body weight of two *Neoscona* species during the period when prey collections were conducted (*N. punctigara*: $y=18.3e^{0.043x}$ *N. mellotteei*: $y=16.0e^{0.031x}$). Date 0 means the first day when prey collection was conducted.

8.0 ± 0.02, $n=11$). No significant differences were found between the species in the response time, weight of wrapping silk and wrapping time (Table 3).

Figure 4 shows changes in the body weight of spiders estimated by the following allometric equations between body length and body weight (*Neoscona puntigera*; $\log Y = 2.962 \log X - 3.931$, $F_{(1,23)} = 547.158$, $p < 0.0001$, *N. mellotteei*; $\log Y = 3.934 \log X - 4.72$, $F_{(1,23)} = 284.655$, $p < 0.0001$) during the prey collection period. *Neoscona punctigera* tended to grow faster than *N. mellotteei* (Fig. 4 Nonlinear mixed-effects model: *N. punctigera*: $y = 18.3e^{0.043x}$, *N. mellotteei*: $y = 16.0e^{0.031x}$, $t = -1.811$, $p = 0.071$).

Discussion

Craig (1987) reported a positive relationship between kinetic energy absorption ability of webs and prey weight captured by the webs in five araneoid species. Here we also found a similar relationship; *Neoscona punctigera* and *N. scylla* showed higher kinetic energy absorption ability of webs and caught heavier prey than the other two species. It is possible, however, that these differences could be due to the differences in prey availability since prey were sampled in different habitats and/or seasons.

Our second approach to compare two sympatric species provided support for the causal relationship between foraging traits and prey items. Firstly, *Neoscona punctigera* showed a higher kinetic energy absorption ability and a higher stickiness of the web than *N. mellotteei*, and captured heavier prey than *N. mellotteei*. Secondly, there were no differences in web placement between the species as well as behavioral traits. The higher kinetic energy absorption ability of webs in *Neoscona punctigera* appears to be adaptive for capturing heavy prey like coleopterans. Higher web stickiness in *Neoscona punctigera* would also appear to be an adaptive trait as coleopterans tend to continuously struggle after being intercepted by a web (Nentwig 1982). However, one may wonder how these differences in web properties (about 1.5 times) could lead to such marked differences in prey compositions between species in this study as some diurnal species can show more than a magnitude difference in web stickiness and show no obvious differences in prey composition (Miyashita 1997). One possible explanation is that, at night when prey diversity is lower than in the daytime (Nyffeler & Benz 1989, Speakman et al. 2000, Basset et al. 2001), even a small difference in a foraging trait may cause a large difference in prey compositions if the trait were to exceed a threshold for capturing prey that are difficult to capture.

To elucidate the general features of prey in nocturnal orb-weavers, we collated data on prey items of nocturnal orb-web species as well as diurnal species from previous studies (tropical species and *Tetragnatha* species are excluded.) (Table 4). Firstly, nocturnal spiders generally captured more Coleoptera than diurnal spiders. These differences may reflect different insect availability between day and night (see Herberstien & Elgar 1994, Spagarino et al. 2001). Secondly, there are substantial differences in the contributions of beetles to the diet of spiders among nocturnal species. This may partly reflect the differences in prey availability between different habitats, seasons, or both.

Table 4. Comparison of main prey items (% by number) between diurnal and nocturnal orb-web spiders. Blank cells mean that its value is included in "Others".

Diurnal

Spider species	Coleoptera	Homoptera	Diptera	Lepidoptera	Hymenoptera	Others	References
Araneus cornutus	1.1	13.7	70.9		6.0	8.2	Nentwig 1983a
Araneus diadematus	1.2	19.0	60.5	0.5	16.9	1.9	Nyffeler & Benz 1989
Argiope aurantia	8.7	0.0	5.8	37.7	27.5	18.8	Uetz et al. 1978
Argiope bruennichii	1.1	27.8	55.2	0.1	13.1	2.7	Nyffeler & Benz 1989
Argiope trifasciata	23.2	8.7	11.6	15.9	18.8	20.3	Uetz et al. 1978
Cyclosa conica	24.0	33.0	33.0		9.0	0.0	Nentwig 1983b
Cyclosa turbinata	1.5	70.6	13.2	0.0	11.8	2.9	Nyffeler & Sterling 1994
Gea heptagon	0.7	62.6	15.6	0.0	15.7	4.9	Nyffeler et al. 1989
Metepeira labyrinthea	44.1	8.9	4.3	1.8	31.0	10.0	Wise & Barata 1983
Nephila plumipes	8.0		60.0	3.0	27.0	3.0	Herberstein & Elgar 1994
Zygiella x-notata	0.0	65.0	30.0		2.0	3.0	Nentwig 1983a
mean	8.9	32.8	33.5	6.6	16.2	6.4	

Nocturnal

Spider species	Coleoptera	Homoptera	Diptera	Lepidoptera	Hymenoptera	Others	References
Acanthepeira stellata	14.4	43.3	30.8	2.9	3.9	4.8	Nyffeler et al. 1989
Araneus quadratus	0.8	13.3	75.8	0.1	8.9	0.9	Nyffeler & Benz 1989
Eriophora transmarina	15.0		30.0	45.0	0.0	13.0	Herberstien & Elgar 1994
Neoscona arabesca	47.0	18.7	18.7	5.8	5.8	3.8	Culin & Yeargan 1982
Neoscona arabesca	31.8	50.0	4.5	4.5	4.5	4.5	Nyffeler et al. 1989
Neoscona mellotteei	17.0	38.3	5.3	5.3	23.9	10.1	This study
Neoscona punctigera	49.3	19.1	2.2	6.6	7.7	15.1	This study
Neoscona scylla	54.3	1.4	7.1	15.7	4.3	17.1	This study
Neoscona scylloides	20.0	24.0	0.0	20.0	12.0	24.0	This study
Nuctena cornuta	2.0	9.8	81.1	0.3	0.4	6.5	Nyffeler & Benz 1989
mean	24.8	28.4	24.3	9.5	6.7	8.9	

However, as we have shown in this study, foraging traits may have contributed to differences in the efficiency of capturing beetles. *Neoscona punctigera*, which consumed more beetles than *N. mellotteei*, tended to show a higher growth rate, suggesting that the spider may benefit by exploiting beetles having large biomass. There is therefore a potentially large selective advantage for beetle specialization in nocturnal environments.

Despite the greater activity of moths at night (e.g. Herberstein & Elgar 1994, Speakman et al. 2000), nocturnal spiders do not always capture large amount of Lepidoptera. The webs of these nocturnal species are of a typical orb-web design that may not have a kinetic energy absorption ability and stickiness needed to capture moths, in contrast to some moth specialized nocturnal species that have unusual web designs e.g. *Pasilobus*, *Mastophora*, *Crytarachne* and *Tylorida*. (see Cartan & Miyashita 2000). It appears that moth specialization may have required a significant shift of foraging strategy while beetle specialization may have required relatively minor changes This difference is probably due to difficulty in catching moth that have scales.

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